VARIATION IN THE SILURIAN TABULATE CORAL *PALEOFAVOSITES ASPER*, AND THE STATUS OF *MESOFAVOSITES*

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ABSTRACT. *Paleofavosites asper* (d'Orbigny) is redescribed on the basis of the holotype and additional material from its type area of the Welsh Borderland. The species shows considerable variation, particularly in the form and location of intercorallite pores, from colonies with pores, including a high proportion of solenia, almost exclusively located in corallite angles to those with up to 40% of pores within corallite walls. This species, the type species of *Paleofavosites* Twenhofel, 1914 includes variants with the structural features considered characteristic of *Mesofavosites* Sokolov, 1951. We therefore regard *Mesofavosites* as a junior subjective synonym of *Paleofavosites*.

PALEOFAVOSITES was erected by Twenhofel (1914, p. 24) for favositid corals with intercorallite pores confined in position to corner locations, that is in the angles between corallite walls. Although he was working on material of Ordovician and Silurian age from Anticosti Island, northern Canada, he identified his species with the European *Favosites asper* d'Orbigny, which he therefore chose as the type species for his new genus.

F. aspera [*sic*] d'Orbigny (1850, p. 49) is *F. alveolaris* Lonsdale (*non* Goldfuss) (1839, p. 681, pl. 15 *bis*, fig. 1, 1*a*, 1*b* only). In contrast to Twenhofel's diagnosis for the genus, Jones (1936, p. 15), who redescribed *F. asper*, recorded occasional pores within the walls of corallites of this species in addition to the abundant pores in corner locations. Jones, however, reported the type specimen as lost and based his revision on other material from the Much Wenlock Limestone of Wenlock Edge and Dudley.

Until quite recently, usage of *Paleofavosites* tended to follow the reported character of the type species, with the inclusion in the genus of species with pores in both wall and corner locations as well as those in which pores are restricted to the corallite angles (e.g. Stearn 1956; Hill 1959; Flower 1961). In his important series of papers on Russian tabulate corals, however, Sokolov (1951, p. 59) erected a new genus *Mesofavosites* for favositids with pores in both wall and corner locations and restricted *Paleofavosites* to the terms of Twenhofel's original diagnosis. Since that time, it has become the common practice of Russian workers, and more recently of specialists elsewhere, to follow this usage (Klaamann 1964; Stasińska 1967; Oekentorp and Schouppé 1969; Oekentorp 1971; Stel 1975). Even so, the presence of occasional pores within the walls is accepted in some species of *Paleofavosites* described by these authors, for example, *P. haapsaluensis* Klaamann (Stasińska 1967, p. 69), *P. oelaensis* Klaamann (Stasińska 1967, p. 71), and *P.* sp. a (Stel 1975, pl. 16). Scrutton (1975, p. 29), however, pointed out that if Jones's redescription of *P. asper* is accurate, then *Mesofavosites* should be considered a junior subjective synonym of *Paleofavosites*. If two groups of favositids, one with pores in both wall and corner locations, and the other with pores in corner locations only, are to be distinguished, then it is the group with pores restricted to

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corner locations that requires the establishment of a new genus. We consider, however, that the range of variation in *P. asper* is such that no generic distinction within this group of corals seems justified.

VARIATION IN PORE POSITION IN *PALEOFAVOSITES ASPER*

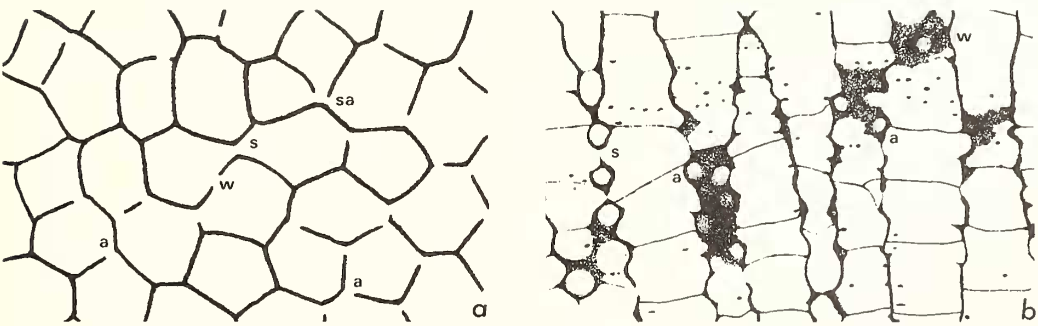
This paper offers a thorough revision of *P. asper* (d'Orbigny) based on a sample of fourteen colonies from the Wenlock and Ludlow Series of the Welsh Borderland and West Midlands. The sample, apart from the holotype and Jones's material, consists of specimens collected by J. H. P. in connection with a revision of British Silurian tabulate corals. The holotype of this species is not missing, as Jones supposed, but is preserved in the Museum of the Institute of Geological Sciences, London (Oekentorp 1971, p. 159). Oekentorp (1976, p. 168) has recently redescribed the holotype only of *P. asper* in the course of a valuable contribution on the definition of the previously confused species *P. asper*, *P. alveolaris* (Goldfuss), and *P. alveolaris sensu* Lonsdale (*non* Goldfuss) (1839, pl. 15 *bis*, fig. 2, 2*a* only) which he assigned to *P. rugosus* Sokolov. He discussed at length the problem of the significance of pore morphology and location but reported no definite pores within the walls of the holotype of *P. asper* and he left the status of *Mesofavosites* open. We are able to demonstrate, however, the presence of occasional pores within the walls of the holotype (Pl. 28, fig. 2). In addition, there is a range among other material of the same species from the Much Wenlock Limestone and Aymestry Limestone of the Welsh Borderland and West Midlands from colonies in which pores in wall locations are extremely rare, to those in which they constitute 40% of pores seen in cross-section (Table 1).

Three varieties of pores are present in the species as a whole, although two types dominate in most colonies. Pores in corner locations are either *solenia*, short tubular pores linking opposite corallites where four corallites meet at a common junction, or *angle pores* linking adjacent corallites (text-fig. 1). In vertical series solenia alternate in orientation through 90°, linking first one pair and then the other pair of opposite corallites to produce a very characteristic pattern in longitudinal section (text-fig. 1*b*; Stel and Oekentorp 1976, fig. 3). Solenia are present in all specimens assigned here to *P. asper*, although they are very rare in BMNH R49779 and R49780. Angle pores are defined as developed in the lateral margin of a corallite wall such that in cross-section they appear bounded by the wall in which they occur on one side only. Such pores are present and common throughout. The third variety of pore is the *wall pore*, contained entirely within one corallite wall (text-fig. 1). These are very rare in nearly half the colonies of *P. asper* described here (Table 1). All three varieties of pores are present in the holotype (Pl. 28, fig. 2). The three pore forms described could all be considered as varieties of mural pores, but there is descriptive value in distinguishing solenia from mural pores in wall and angle locations. The term mural pores is used in this paper in this sense, that is for angle pores and wall pores together.

Within the species, the pores appear to form a continuous morphological series. Solenia can only form at the junction of four corallites. Occasionally 'sub-solenioid' arrangements of angle pores, when a solenium is replaced by one or two angle pores at four corallite junctions, are seen in cross-section, linking these two pore types (text-fig. 1*a*; Pl. 28, fig. 5; Pl. 29, fig. 2). Angle pores at three- and four-wall junctions are as

TABLE 1. Data for the individual colonies and total sample of *Paleofavosites asper*. Although in three colonies, no wall pores were observed within the 2 sq. cm. area from which pore percentages were calculated (indicated by asterisks), in each case at least one wall pore was observed in cross-section outside this area. N = number of corallites; O.R. = over-all range; x̄ = mean; s = standard deviation.

Specimen No.	Corallite Diameter (mm)				Tabulae per 5mm		Angle Pores mean diam (mm)	Pore Percentages in 2 sq cm cross section		
	N	O.R.	x̄	s	unthickened zone	thickened zone		Solenia	Angle Pores	Wall Pores
BMNH R49785	40	0·89 - 1·16	1·02	0·060	5	11	0·16	26	74	0*
BMNH R49787	40	1·02 - 1·32	1·13	0·086	6	10	0·19	22	78	0*
BMNH R49788	40	0·92 - 1·35	1·12	0·081	6	13	0·19	19	81	0*
BMNH R26302 (figd Jones 1936)	40	0·70 - 1·15	0·94	0·087	7	12	0·16	39	60	1
BMNH R49784	40	0·85 - 1·28	1·12	0·129	6	9	0·19	31	68	1
BMNH R49781	40	0·85 - 1·15	1·03	0·066	10	18	0·18	8	91	1
BMNH R49782	40	0·92 - 1·19	1·04	0·069	7	12	0·14	8	89	3
BMNH R49783	40	0·99 - 1·20	1·09	0·050	7	15	0·17	17	79	4
BMNH R49780	40	0·92 - 1·28	1·03	0·087	10	15	0·16	2	91	7
BMNH R49778	40	0·80 - 0·95	0·87	0·034	6	12	0·14	6	85	9
GSM GSb 3728 (holotype)	40	0·90 - 1·29	1·08	0·087	3	6	0·20	12	77	11
BMNH R49786	40	0·86 - 1·12	1·01	0·064	12	15	0·15	7	81	12
BMNH R49779	40	0·87 - 1·21	0·98	0·059	4	12	0·17	2	65	33
BMNH R26559 (descr. Jones 1936)	40	0·92 - 1·35	1·10	0·101	9	23	0·15	5	55	40
TOTAL SAMPLE	560	0·70 - 1·35	1·04	0·079	range 3-12	range 6-23	range 0·14-0·20			



TEXT-FIG. 1. Pore types in *Paleofavosites* in (*a*) cross-section, and (*b*) longitudinal section. s = solenium; sa = 'sub-solenioid' angle pore; a = angle pore; w = wall pore. × 10.

closely packed in vertical series as solenia and are associated with walls with strongly corrugated lateral margins. There is a complete range from angle pores of this description to those in which their vertical spacing is increased, and the wall margins are progressively less corrugated. This can be seen both between and within colonies, whilst in BMNH R26559 wall margins are almost always straight (Pl. 29, fig. 6). Wall pores also show a complete range from locations close to wall junctions to mid-wall situations.

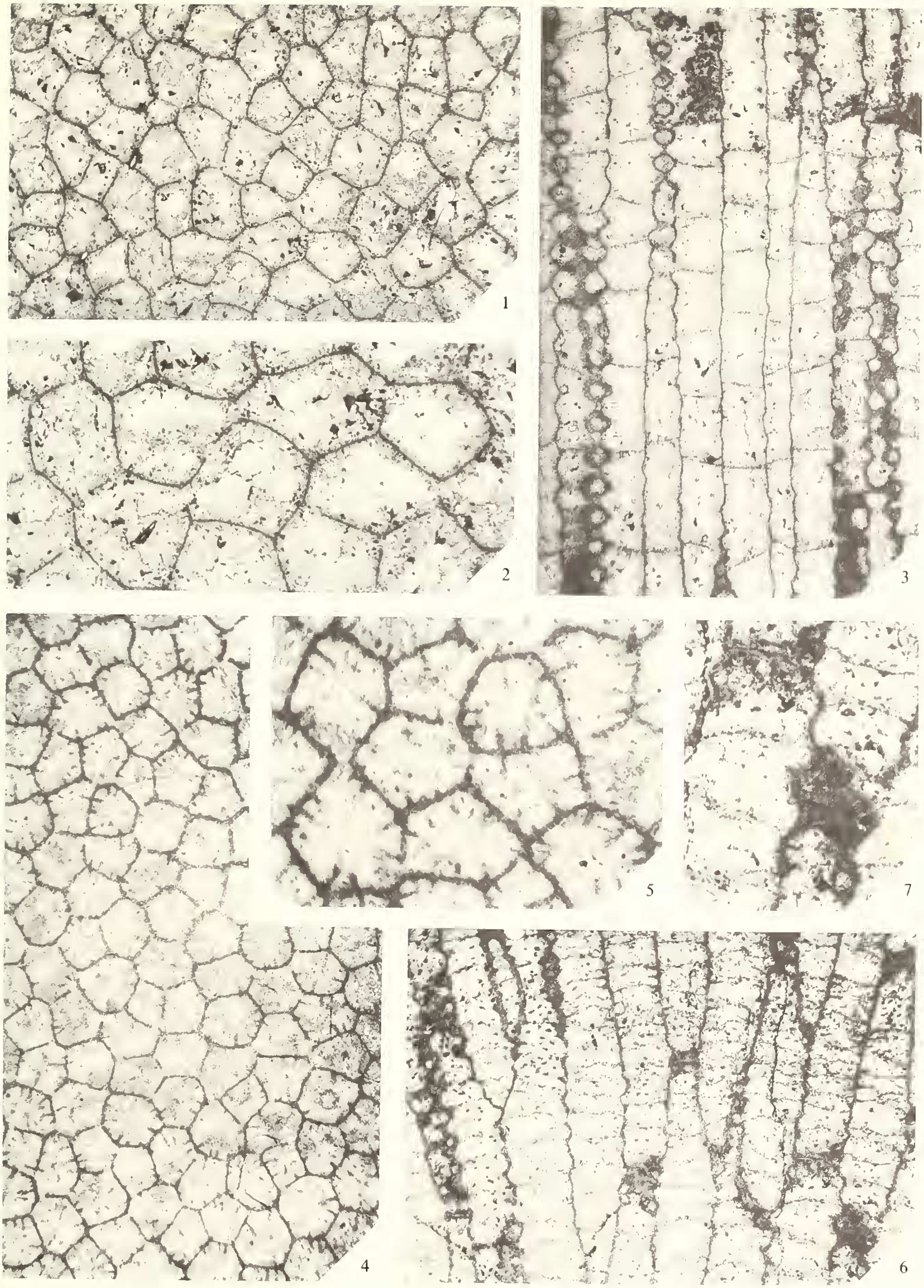
THE STATUS OF *MESOFAVOSITES*

The principal factor in the diagnosis of *Mesofavosites* has been the presence of pores in both angle and wall locations. In addition, the type species, *M. dualis* Sokolov (1951, p. 61, pl. 22, figs. 1–5; pl. 23, figs. 1–2), appears to lack solenia and strongly crenulate wall margins in longitudinal section, although little information on variation in this species is currently available. All of these features, except the total lack of solenia, occur in variants of *P. asper* and none of them can be used as a secure foundation for a generic distinction between *Mesofavosites* and *Paleofavosites*. The absence of solenia may be a function of corallite size as suggested by Stel and Oekentorp (1976, p. 169), with four corallite junctions rare in favositids with larger corallites. There are a number of species with larger corallites assigned to *Paleofavosites* that lack solenia. Furthermore, although Stel and Oekentorp (1976, p. 165) consider the lack of laterally crenulate walls associated with angle pores as distinctive of *Mesofavosites*, this condition is seen in the sample of *P. asper* described here (BMNH R26559). Finally, the corallite walls of *M. dualis* are corrugated in cross-section. Sokolov himself, however, assigned species with straight corallite walls to *Mesofavosites* (*M. multiporus* Sokolov, 1951, p. 69, pl. 29, figs. 3–4) and species with crenulate walls to *Paleofavosites* (*P. legibilis* Sokolov, 1951, p. 13, pl. 2, figs. 7–9; pl. 3, figs. 1–2) and this feature is clearly not of generic significance.

We conclude therefore that *Paleofavosites* should be interpreted broadly to include species with both wall pores and angle pores, as well as those with angle pores only, with or without the development of solenia. In view of the considerable infraspecific variability in pore form and location in the type species, we believe that there is no justification for erecting any generic subdivision within this group of favositids. We consider *Mesofavosites* to be a junior subjective synonym of *Paleofavosites*. In addition, Stel and Oekentorp (1976) have argued that *Multisolenia* Fritz, 1937, *Mesosolenia* Mironova, 1960, *Priscosolenia* Sokolov, 1962 and *Sparsisolenia* Stasińska, 1967, genera based on variations in the development of solenia, are also junior subjective synonyms

EXPLANATION OF PLATE 28

Figs. 1–7. *Paleofavosites asper* (d'Orbigny). 1–2, GSM PF 4787; 3, GSM PF 4788 (holotype). Silurian, Aymestry Limestone, Leinthall Earls, near Aymestrey, Hereford and Worcester. 1, cross-section, × 8; 2, cross-section showing a solenium, wall pore, and angle pore closely associated (slightly left of centre), × 16; 3, longitudinal section showing solenia and angle pores, × 8; 4–5, BMNH R49781a; 6–7, BMNH R49781b. Silurian, Much Wenlock Limestone, Shadwell Rock Quarry, Much Wenlock, Salop. 4, cross-section of colony with well-developed septal spines, × 8; 5, cross-section showing a solenium (left centre) and a 'sub-solenioid' angle pore (right centre), × 16; 6, longitudinal section, × 8; 7, detail of part of fig. 6 showing a wall pore and angle pores, × 16.



POWELL and SCRUTTON, *Paleofavosites asper* of *Paleofavosites*. Although we have not specifically studied examples of these genera, we support these synonymies on the basis of the published information and our observations on *Paleofavosites asper*. Stel and Oekentorp (1976, p. 173), however, go further and suggest that *Multisolenia* is a synonym of *Desmidopora* (Nicholson 1886) and that *Desmidopora* should be maintained as a subgeneric division within *Paleofavosites*. From published information, and in the absence of a full redescription of the type species *D. alveolaris* Nicholson we are not convinced that *Desmidopora* is a paleofavositid: we understand that redescription of *D. alveolaris* is intended for subsequent publication by Stel and Oekentorp (Stel, pers. comm. to J. H. P.). In the meantime, we would point out that if *Desmidopora* and *Paleofavosites* are accepted as congeneric subgenera, then *Desmidopora* has priority and they should be designated *Desmidopora* (*Desmidopora*) and *Desmidopora* (*Paleofavosites*), not as given by Stel and Oekentorp (1976, p. 173) (see I.C.Z.N., Art. 23e).

Our study of *P. asper* illustrates the highly variable nature of favositid species as demonstrated by most work on large samples of these corals (e.g. Philip 1960). Other favositid species from the Welsh Borderland at present under study by J. H. P. also show this tendency to high variability, with adult corallite diameter the least-affected character and apparently the most useful primary species discriminator. Over the years a very large number of favositid species have been erected, often on only a single specimen or a very small sample. It is highly likely that many of these are synonyms and there is a great need for more variation studies of substantial populations of favositids to bring species discrimination in this group to a more realistic level and to stabilize generic concepts.

SYSTEMATIC DESCRIPTIONS

Order TABULATA Edwards and Haime, 1850
Suborder FAVOSITINA Sokolov, 1962
Family FAVOSITIDAE Dana, 1846
Genus PALEOFAVOSITES Twenhofel, 1914

1914 *Paleofavosites* Twenhofel, p. 24.
e.p. 1936 *Favosites*; Jones, p. 2.
1937 *Multisolenia* Fritz, p. 231.
1940 *Palaeofavosites*; Lang, Smith and Thomas, p. 94.
1951 *Palaeofavosites*; Sokolov, p. 12.
1951 *Multisolenia*; Sokolov, p. 50.
1951 *Mesofavosites* Sokolov, p. 59.
1955 *Palaeofavosites*; Sokolov, p. 153.
1955 *Mesofavosites*; Sokolov, p. 153.
1955 *Multisolenia*; Sokolov, p. 153.
1956 *Paleofavosites*; Stearn, p. 59.
1959 *Paleofavosites*; Hill, p. 11.
1960 *Mesosolenia* Mironova, p. 95.
1961 *Paleofavosites*; Flower, p. 71.
1962 *Priscosolenia* Sokolov, p. 58.
1964 *Palaeofavosites*; Klaamann, p. 5.
1964 *Priscosolenia*; Klaamann, p. 40.
1964 *Multisolenia*; Klaamann, p. 42.
1964 *Mesofavosites*; Klaamann, p. 45.

1967 *Palaeofavosites*; Stasińska, p. 66.
1967 *Priscosolenia*; Stasińska, p. 73.
1967 *Sparsisolenia* Stasińska, p. 74.
1967 *Multisolenia*; Stasińska, p. 75.
1967 *Mesofavosites*; Stasińska, p. 76.
1971 *Palaeofavosites*; Oekentorp, p. 158.
1975 *Paleofavosites*; Scrutton, p. 29.
1975 *Palaeofavosites*; Stel, p. 41.
1975 *Priscosolenia*; Stel, p. 55.
1975 *Multisolenia*; Stel, p. 61.
1975 *Mesofavosites*; Stel, p. 65.
1976 *Paleofavosites*; Oekentorp, p. 165 (see for extensive synonymy excluding *Mesofavosites*).

Type species (by original designation). *Favosites aspera* [*sic*] d'Orbigny 1850, p. 49 = *F. alveolaris* Lonsdale (*non* Goldfuss) 1839, p. 681, pl. 15 *bis*, fig. 1, 1*a*, 1*b*, *non* fig. 2, 2*a*.

Diagnosis. Massive, ramose, foliaceous, or encrusting cerioid tabulate corals. Corallites generally contiguous, polygonal, of similar diameter throughout much of their length. Angle pores characteristic but solenia and/or wall pores may also be present in varying proportions. Septal spines present in some species, variably developed, usually in vertical rows. Squamulae also variably developed in some species, with or without associated septal spines. Squamulae and septal spines in the same species usually intergrade. Tabulae generally flat, complete. Increase lateral.

Remarks. As Caramanica (1975) has recently pointed out, the correct, original spelling of the generic name is *Paleofavosites* and not *Palaeofavosites* as used by many authors including Oekentorp (1971) in his submission to the I.C.Z.N. The ruling in favour of the validation of the generic name by the Commission meant that the incorrect spelling was initially placed on the Official List of Generic Names (Opinion 1059). This has since been corrected in *Bull. zool. Nomencl.* **33,** 3/4 (1977), 264.

Paleofavosites asper (d'Orbigny, 1850)

Plate 28, figs. 1–7; Plate 29, figs. 1–6; text-fig. 2; Table 1

non 1829 *Calamopora alveolaris* Goldfuss, p. 77, pl. 26, figs. 1*a–c*.
e.p. 1839 *Favosites alveolaris* (de Blainville) Lonsdale, p. 681, pl. 15 *bis*, fig. 1, 1*a*, 1*b*, *non* fig. 2, 2*a*.
1850 *Favosites aspera* d'Orbigny, p. 49.
non 1851 *Favosites aspera* d'Orbigny; Edwards and Haime, p. 234.
e.p. 1855 *Favosites aspera* d'Orbigny; Edwards and Haime, p. 257, pl. 60, fig. 3, 3*a*.
1914 *Paleofavosites aspera* (d'Orbigny) Twenhofel, p. 24.
1936 *Favosites asper* d'Orbigny; Jones, p. 15, pl. 2, figs. 1–3.
1971 *Palaeofavosites asper* (d'Orbigny); Oekentorp, p. 158.
1976 *Paleofavosites asper* (d'Orbigny); Oekentorp, p. 168, pl. 19, figs. 1–9; pl. 20, figs. 1–3; pl. 21, figs. 7–8, *cum syn.*

Holotype. GSM GSb 3726–3728 (parts of one specimen; slides GSM PF 4548–4551, peels GSM PF 4787–4788). Silurian, Ludlow Series, Aymestry Limestone; Leinthall Earls, 3·2 km NNE. of Aymestry, Hereford and Worcester.

The horizon and locality were given as 'Wenlock Limestone, Leinthall Earls' by Lonsdale (1839, p. 681). The large quarry at Leinthall Earls (SO 44306810), however, is in the Aymestry Limestone (Bringewood Beds) of the Ludlow Series. *P. asper* has been found by us in this quarry (BMNH R49778–49779) and the preservation of the material closely matches that of the holotype. The nearest outcrop of the Much Wenlock Limestone to yield *P. asper* in the present investigation was at Pitch Coppice (SO 47297300), 6 km NE. of Leinthall Earls where the preservation is less similar to that of the holotype. We conclude, therefore, that the horizon of the holotype was wrongly stated by Lonsdale.

Additional material. Silurian, Ludlow Series, Aymestry Limestone: BMNH R49778–49779, large working quarry, Leinthall Earls, Hereford and Worcester (SO 44306810).

Silurian, Wenlock Series, Much Wenlock Limestone: BMNH R26559 and R49780, Farley Quarry, 1·7 km N. of Much Wenlock, Salop (SJ 62900152); BMNH R49781, Shadwell Rock Quarry, 1 km N. of Much Wenlock, Salop (SJ 62620090); BMNH R49782–49783, outcrop in field 120 m W. of Lower Dinchope–Westhope Road, 685 m from Lower Dinchope, near Craven Arms, Salop (SO 45228495); BMNH R49784, disused quarry in Pitch Coppice, near Ludlow, Salop (SO 47297300); BMNH R26302, Dudley, West Midlands.

Silurian, Wenlock Series, Edgton Limestone: BMNH R49785–49788, track to Thrushes Mead, Ridgeway Wood, near Edgton, Salop (SO 39928645).

Diagnosis. Paleofavosites of lamellar to broadly-domed growth form with mean adult corallite diameter in the range 0·87–1·13 mm. Colonies may have regularly developed growth zones of thickened skeletal elements. Corallite wall thickness variable within and between colonies, from 0·09 mm in unthickened zones to 0·15 mm in thickened zones. Septal spines and squamulae very variably developed and intergrading; both more common in thickened zones and rare to absent elsewhere. Angle pores common, solenia usually well developed but occasionally rare, wall pores very rare to moderately common. Pores 0·14–0·20 mm mean diameter. Tabulae complete, horizontal; spacing variable from 3 in 5 mm in unthickened zones to 23 in 5 mm in thickened zones.

Description. The holotype, now in four parts, was an approximately broadly-domed colony 120 mm diameter by 70 mm high. Other specimens range from lamellar to broadly-domed in growth form and reach a maximum size of 230 mm diameter by 80 mm high.

The corallites are polygonal in cross-section, 3–4 sided when immature, 4–7 sided in adult stages. Mean corallite diameter of the sample is 1·04 mm and ranges in colonies from 0·87 to 1·13 mm. Corallite walls are thin in the holotype, 0·09–0·12 mm thick, consisting of an axial plate, 0·02–0·03 mm thick, coated on either side by fibronormal tissue. Regular growth zones of skeletal thickening are present but these are more prominent in most of the other material. They have a vertical frequency of between 4 and 12 mm and walls may reach 0·20 mm thick in thickened zones. Septal spines and flattened, squamulate spines are very variably developed and one form grades into the other. Both are more prominent or sometimes only developed in the thickened zones but even here are usually present only around part of the periphery of any one corallite. Up to twelve spines/squamulae per corallite have been counted in cross-section. They

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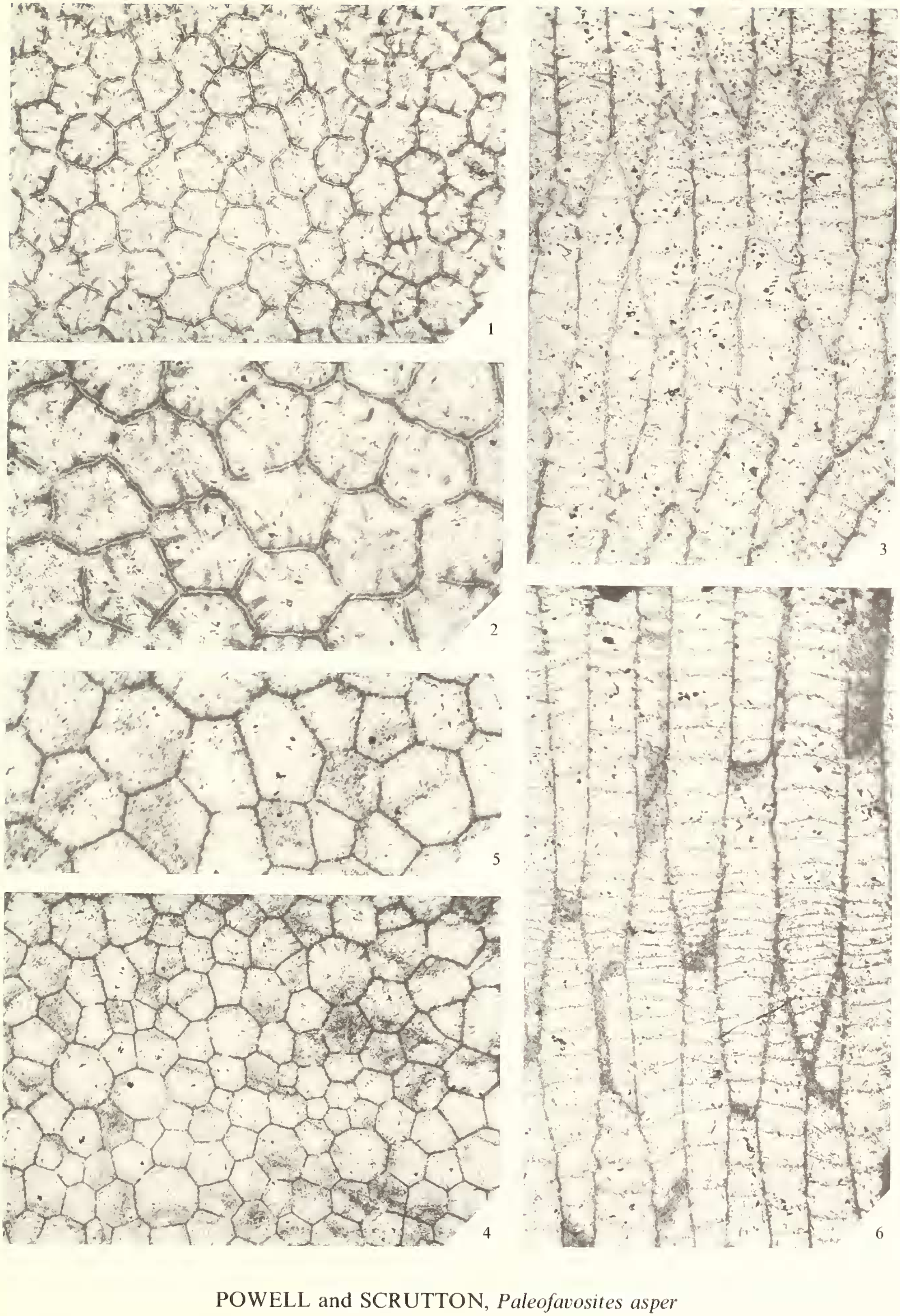
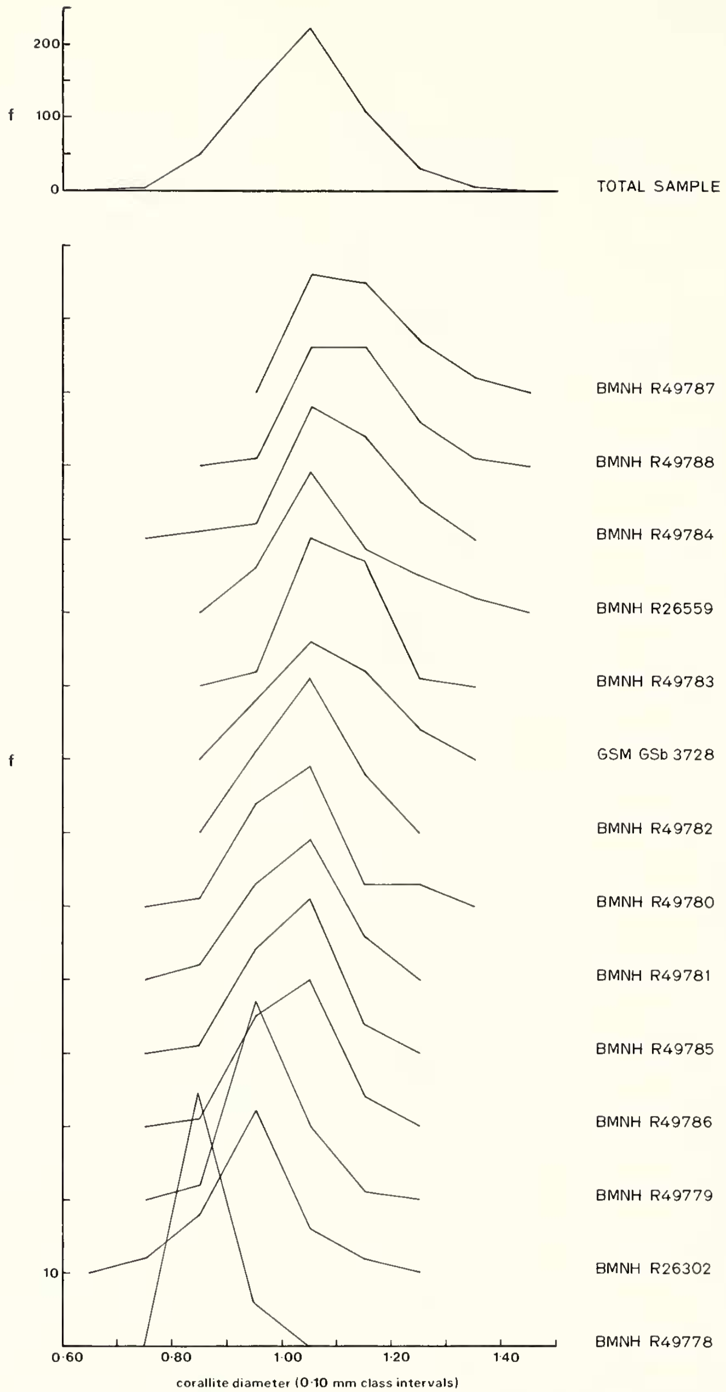
EXPLANATION OF PLATE 29

Figs. 1–6. *Paleofavosites asper* (d'Orbigny). 1–2, BMNH R49780a; 3, BMNH R49780b; 4–5, BMNH R26559c; 6, BMNH R26559d. Silurian, Much Wenlock Limestone, Farley Quarry, Much Wenlock, Salop. 1, cross-section cut through zone of thickening of colony with well-developed septal spines, × 8; 2, cross-section showing solenium (centre), wall pores (centre and right centre), 'sub-solenioid' angle pore (right top), and several other angle pores, × 16; 3, longitudinal section, × 8; 4, cross-section of colony with more weakly developed septal spines, × 8; 5, cross-section showing a solenium (right of centre), angle pores and several wall pores, × 16; 6, longitudinal section showing relatively straight walls and wall pores, × 8.



POWELL and SCRUTTON, *Paleofavosites asper*



TEXT-FIG. 2. Corallite diameter—frequency polygons for the individual colonies and total sample of *Paleofavosites asper*. In the lower series of polygons, each division on the abscissa is equivalent to ten corallites.

may vary from short, thin spines to stout, blunt projections up to 0·5 mm long. Intercorallites connections are in the form of solenia and mural pores (angle pores and wall pores). In a 2 sq. cm. cross-section, there are 55–91% angle pores, 2–39% solenia, and up to 40% wall pores in the material studied (Table 1). Solenia tend to be more common when wall pores are rare. Mural pores and solenia may be sealed by a pore plate.

In longitudinal section, tabulae are complete, horizontal to slightly concave upwards. Zones of closely spaced tabulae coincide with more numerous, thickened septal spines and thickened corallite walls. Tabulae spacing varies from 6–23 in 5 mm in thickened zones to 3–10 in 5 mm in unthickened zones. Mural pores are circular, 0·14–0·20 mm mean diameter in different colonies with a vertical spacing of 0·35–0·40 mm. Wall pores appear only rarely in the plane of section. Angle pores are usually associated with longitudinally crenulated wall margins, although in some specimens the crenulation may be slight or even absent. Solenia appear as a vertical series of regularly spaced but unconnected rings of skeletal tissue. Septal spines/squamulae are directed horizontally or slightly upwards into the lumen. A circular cross-section is more common than a flattened one, and some spines may change from the former to the latter along their length.

Discussion. Data for the sample described here are listed in Table 1 and illustrated in text-fig. 2. We have used the formula given by Sutton (1966) for the 'diameter' of a polygonal corallite, that is half the sum of the maximum corner-to-corner measurement and the minimum wall-to-wall measurement for each corallite.

P. asper is a very variable species. We regard the development of regular thickened growth zones in these colonies as an environmental feature reflecting an annual climatic cycle. The variation in the development of the septal processes and the spacing of the tabulae is associated with this periodicity, and these morphological elements therefore have limited taxonomic value at the species level in this group of corals. Septal processes are particularly variable in form in *P. asper* to the extent that spines and squamulae show complete intergradation. This is in agreement with Philip's (1960) conclusions that squamulae are modified septal spines subject to environmentally induced variation and of little taxonomic significance. Adult corallite diameter is much less variable and appears to be a more reliable first criterion for species discrimination. Similar conclusions were reached by Sutton (1966).

Schouppé and Oekentorp (1974) also suggested that pore diameter in favositids remains constant within the species and may be of taxonomic value. We find, however, a considerable variation in mean pore diameter from colony to colony of this species (Table 1). Neither is there a strong correlation of mean pore diameter with mean corallite diameter ($r = 0{\cdot}58$).

The feature of this species which we most wish to stress is the considerable variation in pore distribution. Although the proportions of different pore types show little variation from place to place within a colony, there is considerable variation between colonies (Table 1). Other species of *Paleofavosites* from the Welsh Borderland show similar variation in pore location.

P. asper is distinguished from *P. rugosus* Sokolov (= *F. alveolaris* Lonsdale (*non* Goldfuss) 1839, pl. 15 *bis*, fig. 2, 2*a*), which is also present in the Much Wenlock

Limestone of the Welsh Borderland, by its smaller mean corallite diameter (Oekentorp 1976, p. 172). *P. rugosus* in the Welsh Borderland sample has adult corallite diameters in the range 2·10–2·60 mm.

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